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Saccadic Reaction Times in Gap/Overlap Paradigms: a Model Based on Integration of Intentional and Visual Information on Neural, Dynamic Fields

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The systematic variations of regular saccadic reaction times induced in gap/overlap paradigms are addressed by a quantitative model. Intentional and visual information are integrated on a retinotopic representation of visual space, on which activity dynamics is related to movement initiation. Using a specific conception of "motor preparation", known effects of general warnings and fixation point on- and offsets are reproduced. Results of new experiments are predicted and the extent to which fixation point offsets are specific to ocular responses is analyzed in the light of the exposed model architecture. Relations of the theoretical framework to neurophysiological findings are discussed.

Saccades Gap effect Reaction times Fixation Neural field

1. INTRODUCTION

If subjects are instructed to react to the appearance of a go signal with a fast movement of their eyes, then reaction times are observed which are much longer than hypothetical conduction delays. The saccadic reaction time (SRT) is known to depend on several external and internal factors. If subjects track a fixated light spot stepping to an unpredictable position, then typically mean SRTs ranging from 180–250 msec are observed. If the offset of the fixation point (FP) precedes target onset by a certain gap interval, mean SRTs of visually guided saccades can be reduced considerably in humans (down to 100–140 msec) and in monkeys (down to 70–130 msec) (Saslow, 1967; Ross & Ross, 1980; Fischer & Boch, 1983; Fischer & Ramsperger, 1984; Reulen, 1984a; Kalesnykas & Hallet, 1987; Wenban-Smith & Findlay, 1991; Reuter-Lorenz, Hughes & Fendrich, 1991). This "gap effect" could also be observed using an auditory signal preceding target onset without changing a fixated stimulus (Ross & Ross, 1981).

By contrast, a prolongation of mean SRTs is observed as compared to reactions to target steps if the FP overlaps in time with the target (Saslow, 1967; Ross & Ross, 1980; Reulen, 1984a; Boch & Fischer, 1986; Kalesnykas & Hallet, 1987). Here, SRTs are often found to be longer than 250 msec. Importantly, the actual mean SRT depends on the overlap interval (time from target onset to FP offset) in a graded fashion. The functional dependency of SRTs on the gap interval and on the amount of overlap, respectively, can even be lumped together to form one continuous gap/overlap curve, so that an overlap interval can be interpreted conceptually as a negative gap interval. Furthermore, not only a continuously present fixated object can increase SRTs in comparison to gap conditions. Also, its (re-)appearance or change in shape shortly before, as well as up to 150 msec after, target onset is known to increase SRTs effectively (Ross & Ross, 1980; Braun & Breitmeyer, 1990).

The reduction of SRTs in the gap paradigm was further differentiated on the basis of bimodal SRT distributions. The fast mode, near 80 msec in monkeys and 110 msec in humans, has been termed *express* mode, whereas the second part of the bimodal SRT distribution has been referred to as *regular* mode (Fischer & Boch, 1983; Fischer & Ramsperger, 1984). The phenomenon of express saccades turned out to be fragile in humans. Large differences between subjects can be observed and some authors failed to reproduce bimodal SRT distributions at all (e.g. Wenban-Smith & Findlay, 1991; Kingstone & Klein, 1993b). Although the occurrence of express saccades is favored by the gap paradigm, the introduction of a gap is not a necessary condition to observe the express mode. Express movements can even be made in overlap conditions using trained subjects (Boch & Fischer, 1986) or during nearly natural scanning behavior (Sommer, 1994). The fact that certain

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necessary conditions are required to observe express saccades can be used to distinguish them operationally from regular saccades: express responses cannot be made to continuously present targets (Boch & Fischer, 1986; Rohrer & Sparks, 1993), to targets appearing concurrently with other visual features (Nothdurft & Parlitz, 1993; McPeek & Schiller, 1994), or to "anti-targets" in the anti-saccade task (Fischer & Weber, 1992). Thus, although gap conditions favor express saccades, they can be viewed as independent responses, the occurrence of which can be decoupled (e.g. by training) from the reduction of regular SRTs.

Aside from the relative timing among warning events and target onset, SRTs can be prolonged by more complex stimulus configurations requiring a target selection (e.g. Ottes, van Gisbergen & Eggermont, 1984; Heywood & Churcher, 1980). Furthermore, expectation about the upcoming target location based on prior knowledge can reduce SRTs (Kowler, Martins & Pavel, 1984). Also, physical stimulus parameters, like intensity, are known to influence reaction times strongly (Wheeless, Cohen & Boynton, 1967).

The aim of the theoretical study presented here, is to propose a quantitative framework which is able to integrate the action of visual events with behaviorally relevant information imposed onto subjects by the experimental task. Specifically, effects on the latency of regular saccades in gap/overlap paradigms are addressed where general warnings and FP off- and onsets precedes, or follows the appearance of a visually defined target. To make the terminology unambiguous, I refer to the "gap effect" as the latency reducing effect of an arbitrary warning signal on regular saccades and view the generation of express saccades as an independent process, which is, however, usually coupled to the generation of regular saccades. It is the gap effect in regular saccades which is addressed by this study. Below, the different identified components which contribute to the gap effect will be discussed. I leave aside contributions of processes of target selection, effects of prior knowledge as well as variations in physical stimulus parameters. By using the concept of dynamic fields and topographic mappings I show that SRTs can be understood as a reflection of dynamic changes of activity configurations on these fields under the combined action of intentional and sensory information. Due to the inherent presence of representations of visual space within the exposed framework it is possible to address behaviors showing a discrepancy between visual target information and intended movements as required in the anti-saccade task.

As a concrete mathematical implementation of the dynamic field idea, the "neural field" equation proposed by Amari (1977) is used, which had been applied in a theory of self-organizing mappings in primary sensory cortex (Amari, 1989). The dynamic field framework is developed from functional principles (derived from behavioral data), but, due to the model's phenomenology, relations to neurophysiological findings can be discussed. For instance, the consistent treatment of intentional information within the model suggests a specific mechanism of "motor preparation" within neural structures relevant for saccadic movements.

2. BEHAVIORALLY RELEVANT FACTORS IN GAP/OVERLAP PARADIGMS

As reviewed in the Introduction, the gap effect has been studied with a variety of different signals preceding target onset. To incorporate these results into a model, it must be analyzed, which of these events must be seen as acting qualitatively different and which must be seen as being interpreted equivalently by the saccadic system. Reulen's experimental and theoretical results (1984a, b) support the view that it is not the presence or absence of an FP *per se* which affects SRTs, but that it is the transient offset event which is responsible for the reduction of reaction times. This was concluded, for instance, from the fact that SRT distributions in conditions of no FP and a continuously visible FP appeared to be similar. In contrast to the reducing effect of FP offsets, its onset acts in a more complex way onto SRTs. Ross and Ross (1980) showed that for positive gap intervals the onset reduces SRT (but less effective than offsets) but for negative gaps (overlaps) down to -200 msec, SRTs are increased as compared to conditions where the fixation point had not been changed. This led these authors to assign a dual role to the onset event. The first is to act as a general warning signal used by the saccadic system to start the preparation of an eye movement before target onset. They showed that this alerting event also reduces reaction times of manual responses (Ross & Ross, 1981). The second role is specific to saccades. The onset interferes with an ongoing motor preparation by virtue of the visual transient itself.

Recently, more evidence for the existence of two components contributing to the gap effect has been accumulated. For example, Kingstone and Klein (1993a) distinguished between a "fixation offset effect" and a "preparation effect". The latter is relevant, for instance, using peripheral offsets which affect ocular, as well as manual responses, whereas, in addition to the preparation effect, the fixation offset effect is observed for ocular responses only. Further, Reuter-Lorenz *et al.* (1991) found that the fixation offset effect is specific to visually guided saccades. They also used FP offsets separated by a gap interval from target onset, but controlled for the preparation effect by using an additional acoustic tone as a warning. They found that the offset reduced SRTs in visually guided conditions, but gave no further benefit in the anti-saccade task (but, see Fischer & Weber, 1993, p. 598, and the Discussion section below).

Therefore, three different behaviorally relevant types of information will be distinguished when addressing gap/overlap paradigms: (1) FP offset, (2) FP onset, (3) general warning events. It is important to note that the preparation effect associated with general warning events is related to the very artificial restrictions imposed

onto subjects by the paradigms used to study the behavior in gap conditions. Subjects are, of course, *instructed not to move* until a certain go signal is perceived. Without any instruction, a subject is likely to react immediately with an eye movement to, for instance, the onset of a tone. Even the sudden disappearance of a fixated object would naturally evoke saccades aimed at finding the lost object of interest. It is the subject's *intention not to move*, imposed by instruction, which suppresses this kind of behavior. Thus, the preparatory effect is intimately linked to the way saccades (and other movements) are controlled voluntarily. Similarly, without instruction, the sudden appearance of an object at a currently fixated location is likely to suppress saccades into the periphery, or even might cancel an ongoing motor preparation. Thus, due to the instruction to move despite the foveal onset, the FP onset effect is likely to be a reflection of an interference between the suppressing effect of the visual onset and the subject's *intention to move* to the periphery. Consequently, every theoretical framework addressing gap/overlap data has to deal with the action of intention. Then, the way intentional information is dealt with will be nothing but a definition of the vague term "motor preparation".

3. THEORETICAL FRAMEWORK. INTEGRATION OF INTENTIONAL AND SENSORY INFORMATION

Before developing the concrete model, first the assumptions and requirements used to select an adequate theoretical framework are listed:

(1) The total SRT is composed of three different contributions, which are afferent delay, "processing time", and efferent delay. The processing time depends on the behavioral situation and the history of the saccadic system (e.g. when a warning event had appeared). The introduction of a separate processing time is justified by estimations of afferent and efferent transmission delays. Becker and Jürgens (1979) estimated the average sum of afferent and efferent delays to be about 80 msec based on results from double-step paradigms. Here, the target steps twice, where the second step is separated by a variable time interval from the first step. Smit and van Gisbergen (1989) estimated a mean total delay of 50 msec when interpreting the latency transitions in properties of velocity profiles. Throughout this study, afferent and efferent delays are estimated by 40 and 30 msec, respectively. This results in a processing time of the order of 100–200 msec when referring to regular SRTs in gap/overlap paradigms. This clearly shows that aside from transmission delays, time constants are involved, which determine the speed of processes relevant for movement initiation.

(2) To model processing times, a variable $u(t)$ is introduced as a time dependent descriptor of the state of the saccadic system relevant for movement initiation. Further, a criterion is required which is dependent on the actual value of $u(t)$, and is used to initiate the movement. One may think of $u(t)$ as representing a kind of readiness, which, when exceeding some threshold criterion, initiates the movement. A time-course of $u(t)$ can be dealt with by defining *dynamics* of $u(t)$ (i.e. a differential equation), which represents a rule for the temporal evolution of readiness:

$$\tau_u \dot{u}(t) = F[u(t), f_{\text{ext}}(t)]. \quad (1)$$

$F(\cdot, \cdot)$ is some function which remains to be specified and τ_u is a characteristic time constant* determining the rate of change of $u(t)$. $f_{\text{ext}}(t)$ represents external influences. To give an idea in which way the processing time could be accounted for, for instance, the choice

$$\tau_u \dot{u}(t) = -u(t) + f_{\text{ext}} \quad (2)$$

results in an exponential relaxation of $u(t)$ to f_{ext} with the relaxation time τ_u. When $u(t)$ crosses a threshold during its relaxation, the movement starts after the additional efferent delay. Within the large variety of models of reaction times (mostly addressing statistical properties), the combination of dynamics and threshold used here is close to the description proposed and analyzed by Pacut (1977).

(3) Aside from the temporal aspect of processing times, I want to address spatial aspects relevant for gap/overlap paradigms like, for instance, the response specificity of the fixation offset effect. Thus, u must not only depend on time, but also on the retinal coordinate, x. The variable $u(x, t)$ is now called a *field*, or, with respect to the dynamics to be defined, a *dynamic field*. It codes for a readiness for movement to a location defined by the displacement, x, relative to the fixation direction.† For simplicity, only one-dimensional movements (e.g. along the horizontal meridian) are considered so that x represents the amplitude of a possibly upcoming movement.

(4) I distinguish between visual information $f_{\text{vis}}(x, t)$ and *intentional information* $f_{\text{int}}(x, t)$, both acting additively onto the readiness dynamics:

$$\tau_u \dot{u}(x, t) = F[u(x, t)] + f_{\text{int}}(x, t) + f_{\text{vis}}(x, t). \quad (3)$$

Both types of information can specify movement goals by having a local maximum around the location the movement is aimed at.‡ In this way, $u(x)$ can be raised over threshold at locations specified by intended, or visually defined targets. The reasoning behind equation (3) is depicted in the block diagram Fig. 1. Within the box labeled "instruction", sensory signals are interpreted as warnings or go signals and converted into spatial and temporal aspects of $f_{\text{int}}(x, t)$. This transformation level lies outside my theoretical treatment, so that in

*Here, I parameterize explicitly the timescale by τ_u to make the relation of dynamics to processing times more obvious. Clearly, the right-hand-side of equation (1) contributes as well to time constants of the dynamics. But, given a functional form for $F[u, f_{\text{ext}}]$, τ_u can be used to adapt the overall time scale.

†For purposes of this study there is no need to distinguish between retinal coordinates and motor coordinates (displacements).

‡I assume the presence of a well-defined visual target (as is usually the case in gap/overlap paradigms) as well as a unique intention to move somewhere. Thus, $f_{\text{vis}}(x)$ and $f_{\text{int}}(x)$ show only one maximum, respectively, specifying the movement goal.

simulations, the spatio-temporal behavior of f_{int} will be based on assumptions described below. Visual information is coupled also directly to the readiness dynamics to be able to include the FP on/offset effects independent from the preparation effect, which is related to the instruction level.

Due to the spatial model layout, the intention $f_{int}(x)$ can be peaked around $x = 0$, which corresponds to an intention to displace the eyes by a vanishingly small amount. In other words, f_{int} can represent an *intention not to move*. I will refer to this configuration as having an *intention to fixate*. A problem arises if the intentional goal is different from the visual goal. This is relevant basically in two situations. (i) A peripheral visual target appears but the intention is to fixate. In some way intention must be able to suppress the action of visual information, not to raise the field over threshold at a peripheral location. (ii) The visual goal does not match the intentional goal as happens in the anti-saccade task. Again, the action of visual information must be suppressed. The following section presents a solution to this problem by introducing an adequate spatial interaction within the field.

3.1. Lateral inhibition dynamics: neural, dynamic fields

To see how the dominant role of intention can be accounted for, imagine the situation where the intention is to fixate regardless of visual disturbances. If, at a certain time, a visual non-target appears, $f_{vis}(x)$ will be peaked around the corresponding location, but must not raise the field over threshold. On the other hand, having no intention to fixate but an intention to move to the visually defined location, shall result in a movement. Thus, the field at peripheral locations must be further from threshold during fixations as compared to conditions of intended movements. This can be implemented by using a *lateral inhibitory interaction* which shapes

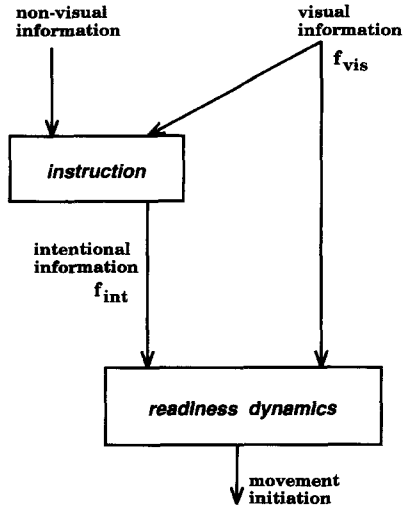

FIGURE 1. Relation among types of behaviorally relevant information and readiness dynamics. Whereas visual information acts directly onto the readiness dynamics, the temporal and spatial aspects of intentional information are the result of an interpretation of sensory signals following a given instruction.

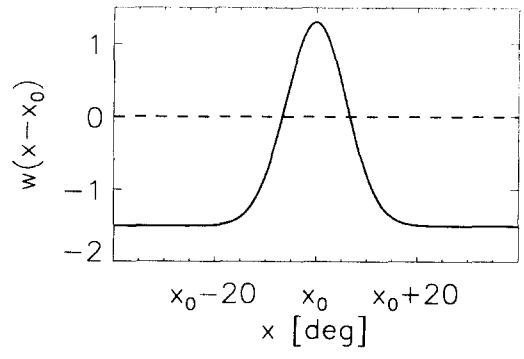

FIGURE 2. Lateral interaction within the field. The graph shows how neighboring locations are influenced if an arbitrary location x_0 of the field is excited (brought over threshold).

the peripheral part of the field dependent on the field near central locations (around $x = 0$). One realization of this idea uses a well-known form of lateral inhibition dynamics:

$$\tau_u \dot{u}(x, t) = -u(x, t) - u_0 + \int_R w(x - x')S[u(x', t)]\,dx' + f_{int}(x, t) + f_{vis}(x, t). \quad (4)$$

τ_u determines the overall time scale as discussed above. $S(u)$ is a threshold function which takes on two values only: $S(u) = 0$ for $u \leqslant 0$ and $S(u) = 1$ for $u > 0$. u_0 is a constant parameter and $w(x)$ is a function specifying the lateral interaction within the field. The parameter R determines the interval of movement amplitudes over which the field extends. Equation (4) can be seen as a spatial generalization of equation (2). It combines the simple relaxation idea (represented by the terms $-u(x, t) - u_0$) with the requirement to deal with possibly conflicting visual and intentional movement goals. The spatial shape of external information is parameterized by Gaussians:

$$f_{int}(x) = k_{int} \exp[(x - x_0)^2/(2\sigma_{int}^2)],$$
$$f_{vis}(x) = k_{vis} \exp[(x - x_0)^2/(2\sigma_{vis}^2)]. \quad (5)$$

Here, x_0 specifies the location of maximal input. The action of the intra-field interaction is now discussed in detail.

To implement the idea of lateral inhibition, the following parameterization of the interaction kernel, $w(x)$, is used:

$$w(x) = k_u \exp[-x^2/(2\sigma_u^2)] - H; \quad H > 0. \quad (6)$$

This is a Gaussian with amplitude k_u and width σ_u, from which a constant, H, is subtracted. The shape of this interaction profile is shown in Fig. 2. Closely spaced field points excite each other, whereas more distant parts inhibit each other. Importantly, the interaction within the field is solely mediated by suprathreshold values of $u(x)$, with respect to the threshold function $S(u)$. As will be shown below, the threshold is related to the criterion *when* to start the movement. I use the term *activity distribution* for $S[u(x)]$ and I will refer to a

suprathreshold region on the field as *activated region*. The functional role of most of the parameters introduced is discussed in the following sections. The role of parameters of minor importance, as well as the numerical procedures are described in the Appendix. There, a table with all parameter values used is also given.

The lateral inhibition dynamics used here had been studied analytically by Amari (1977) with respect to the existence and stability of stationary solutions of the autonomous dynamics (i.e. without external input). The dependence of the width of activated regions on parameters as well as conditions for the existence of self-generated activity has been derived. Following Amari, I refer to the particular equation (4) as *neural* field dynamics.* Recent applications of this framework were in the field of the self-organization of topographic mappings (review Amari, 1989), the modeling of the optic tectum of frogs and toads (Chipalkatti & Arbib, 1987; House, 1988), and the integration of stereo cues (Amari & Arbib, 1977; Chipalkatti & Arbib, 1988). In the context of saccadic motor planning, Kopecz and Schöner (1995) used dynamics fields to model the action of visual information and expectation based on prior knowledge onto the metrics of saccades.

Due to Amari's results, properties of the neural, dynamic field can be designed parametrically. The relevant results of this analysis are reviewed in the Appendix. Briefly, three different parameter regimes can be distinguished according to the stationary behavior of the autonomous dynamics (i.e. without external input): (1) only one homogeneous, subthreshold, stationary solution exists to which all initial conditions relax; (2) a bistable regime, where the homogeneous, subthreshold solution coexists with an inhomogeneous solution, which evokes one cluster of activity; (3) only the inhomogeneous solution exists, again evoking a cluster of activity. In the context relevant here, the latter parameter regime is used, in which all initial conditions relax to an inhomogeneous equilibrium state producing a cluster of *self-generated* activity, which persists even without external inputs. I return to a discussion of this choice in Section 4.1.

Figure 3 depicts the basic field behavior relevant for the initiation of a saccade. To demonstrate the basic properties of field dynamics, the time-course of intentional and visual information is simplified as compared to complete gap/overlap simulations to be described below. The temporal field evolution is shown for two conditions. The left and right column depicts the field behavior under conditions of fixation and no fixation, respectively. Starting at time $t = 0$ (top panels), field distributions are plotted every 56 msec. The dashed lines indicate the zero level. If the field is raised over this threshold, activity is evoked at the corresponding locations, according to the threshold function $S[u(x)]$ in equation (4). In the fixation condition, intentional information acts onto the central field locations (around $x = 0$) evoking a cluster of activity, which in turn inhibits the peripheral parts of the field due to the lateral interaction (left column, top panel). At $t = 50$ msec, a peripheral input (which could be related, for instance, to a visual distractor) centered at 35° is applied to the field, without removing the intention to fixate. During the course of time, peripheral information shapes the field accordingly, but is not able to raise the field over threshold in the periphery. In the second column, no central intention acts onto the field. However, according to the chosen parameter regime, a small amount of activity is present on the field for $t = 0$. This amount is smaller than under conditions of fixation, so that the peripheral field is now less inhibited. Consequently, applying the same peripheral input as in the fixation condition, now results in the creation of peripheral activity (in the fourth panel from top), which in turn suppresses central activity due to the competing effect of the lateral interaction. Thus, in fixation conditions the creation of peripheral activity can be suppressed much more effectively as compared to conditions of no

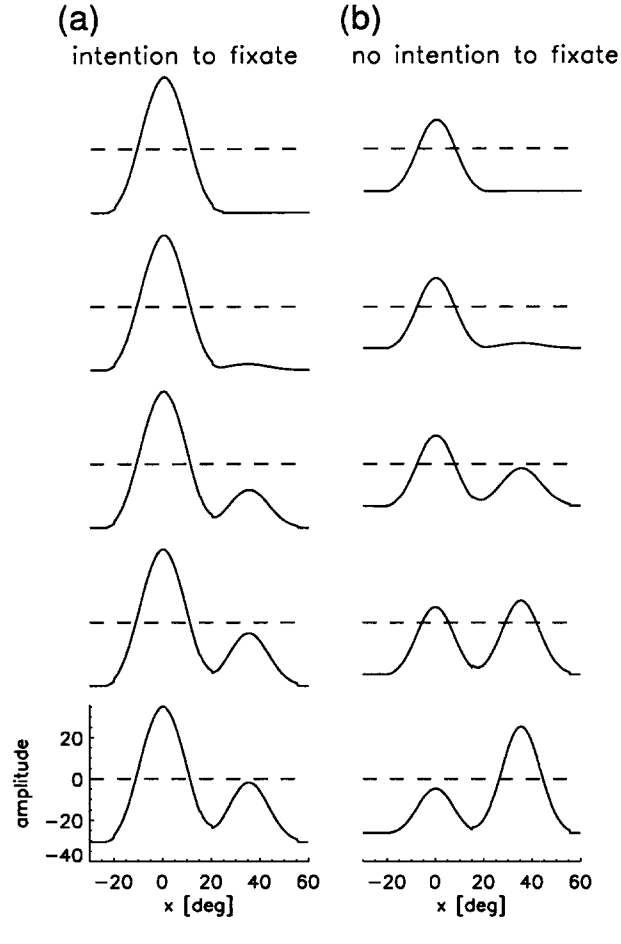

FIGURE 3. Temporal evolution of the field in response to peripheral input in conditions of fixation (a) and no fixation (b). A field distribution is shown every 56 msec, starting with $t = 0$ for the top panels. The peripheral input is applied at $t = 50$ msec. For details, see Section 3.1. In the model, no units are associated with field amplitudes.

*The particular mathematical form of field dynamics cannot be uniquely related to the underlying assumptions. Other mathematical realizations are possible. It is the fact that the neural field can be analyzed analytically which led to this choice.

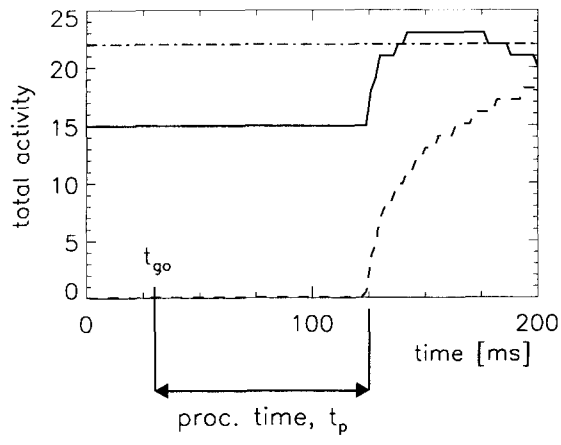

FIGURE 4. Temporal evolution of total activity and total, spatially weighted activity, according to Fig. 3. A peripheral input arrives at the readiness dynamics at time t_{go}. Dashed–dotted line: total activity on the field related to Fig. 3(a). No change is observed due to the persisting central activity. Continuous line: total activity related to Fig. 3(b). It takes the time t_p for the peripheral input to raise the peripheral field over threshold, which is signalled here by an increased total activity (for some time, central and peripheral activity coexist). Dashed line: the total, spatially weighted activity can be used as a simple measure of the mean deviation of activity from the central position. The time this quantity deviates from zero measured from the time of go signal reception is taken as the processing time, t_p (the weighted activity is plotted without a scale, because here, only its deviation from zero is important). The time t_{go} does not represent the time the physical go event appears, but represents the time this go signal is received by the readiness dynamics. The origin of the time axis only indicates the start of the simulation. It is not related to the time of physical target onset. In the model, no units are associated with activity measures.

fixation. In this sense, an intention to fixate can suppress unwanted movements.

The temporal evolution of global activity measures corresponding to Fig. 3 is shown in Fig. 4. The depicted time-courses of total activities are gained by integrating $S[u(x, t)]$ over the spatial field dimension, x. Due to our simple all-or-nothing definition of activity, the total activity can only change in unit steps. The dashed–dotted line depicts the total activity related to the left column in Fig. 3. It is just a constant because the activity configuration was not changed by the peripheral input. The evolution of total activity related to the no fixation condition in Fig. 3 is plotted as a continuous line. For small times, the total activity is related to activity at the field center. At the time the field is raised above threshold at the peripheral location, the activity configuration changes. Peripheral activity grows at the cost of central excitation, which eventually disappears. The dashed line in Fig. 4 represents the criterion to initiate the movement. The total activity would not be an adequate choice, because an intention to fixate evokes activity as well. A criterion is required, which measures the deviation of activity from the central position. A simple measure compatible with this requirement is the total, spatially weighted activity, P, defined by:

$$P = \int_R xS[u(x)]\,dx. \tag{7}$$

The time-course of P is plotted in Fig. 4 in dashed style. It shows a clear increase from zero at the time the peripheral input evokes activity. In the following, the time between the arrival of the peripheral input at the readiness dynamics (t_{go} in Fig. 4) and the time when P deviates from zero is taken as the processing time, t_p. The total SRT then is derived by adding 70 msec transmission delays.

The basic feature that will be responsible for a preparation effect in the model is that for a fixed set of parameters, the time, t_p, it takes to raise the peripheral field above threshold depends on the amount of central activity at the time of peripheral input's onset. This central activity determines the amount of inhibition in the periphery, which has to be overcome by the peripheral input. The more the periphery is inhibited the longer it takes to raise it above threshold.

3.2. Time-course of intentional information: the preparation effect

I now turn to the time-course of intentional information in relation to external events, like warnings, or target onset. Referring back to Fig. 1, this time-course is thought to be generated by the processing stage labeled "instruction", for which, here, no dynamical model is given. Thus, this time-course must be based on assumptions, which are motivated now. In the gap paradigm, subjects are instructed to avoid any movements before the target appears. Thus, first, they have an intention to fixate. A crucial point within the model is now the postulate, that *when a warning is perceived, subjects remove their intention to fixate.* In this sense, they prepare for the movement to the upcoming target. So, within the framework exposed here, *motor preparation* is defined as removing the voluntary response suppression. This does not imply that subjects, at this time, must have an intention to move somewhere. Here, an intention to move to a peripheral location is applied not until the go signal is received by the level relevant for intentional processing (the box "instruction" in Fig. 1). When the FP steps to a peripheral location to act as a target, removing the intention to fixate and applying the peripheral intention occur simultaneously. In the gap task, removing the response suppression and intending to move to a target become temporally segregated. Due to the given instruction, the intention to execute the visually guided movement is not established until target information has been received.

The suggested time-courses in the gap task of intentional and visual information as well as of the resulting field states are shown in Fig. 5. No fixation on/offsets are applied, so that the pure preparation effect can be seen. Conditions with a gap of 0 msec (left column) and 100 msec (right column) are compared. In the 100 msec gap condition, the warning signal is perceived at time t_w. Consequently, the intention to fixate is set to zero ("f_{int} central" in the figure). The activity, which is at that time

self-generated amount (bottom panel). Concurrently, the located at the field center, starts to decay towards the field amplitude, $u(t)$, at the peripheral locations increases towards the threshold, due to the decreasing inhibitory action of the centrally located activity (second panel from bottom). At the time visual target information is received (t_{go}), visual as well as intentional information act onto the corresponding peripheral field region and pulls the peripheral field towards the threshold (for the transient time-course of visual information, see next section). This threshold is crossed earlier in the 100 msec gap condition than in the 0 msec condition, because during the 100 msec gap, the central activity has already decayed to a certain amount which leads to less inhibited peripheral parts. The creation of peripheral activity is detected by a sudden increase of the total, spatially weighted activity, $P(t)$ (bottom panels, dashed lines).

The resulting dependence of the processing time t_p on the gap interval is the equivalent of the preparation effect observed in experiments. SRTs as a function of the gap interval are shown in Fig. 6. The gap interval cannot be extended to negative values here, i.e. to overlaps, because, per definition, a warning event informs the subject about a following target appearance. If the sensory signal used as a warning in gap conditions (which are here at first different from an FP on/offset, e.g. an acoustic tone) is given after the target had appeared, then the target onset itself will serve the function of a warning. In other words, presenting the warning after the target, would not increase SRTs further. This was

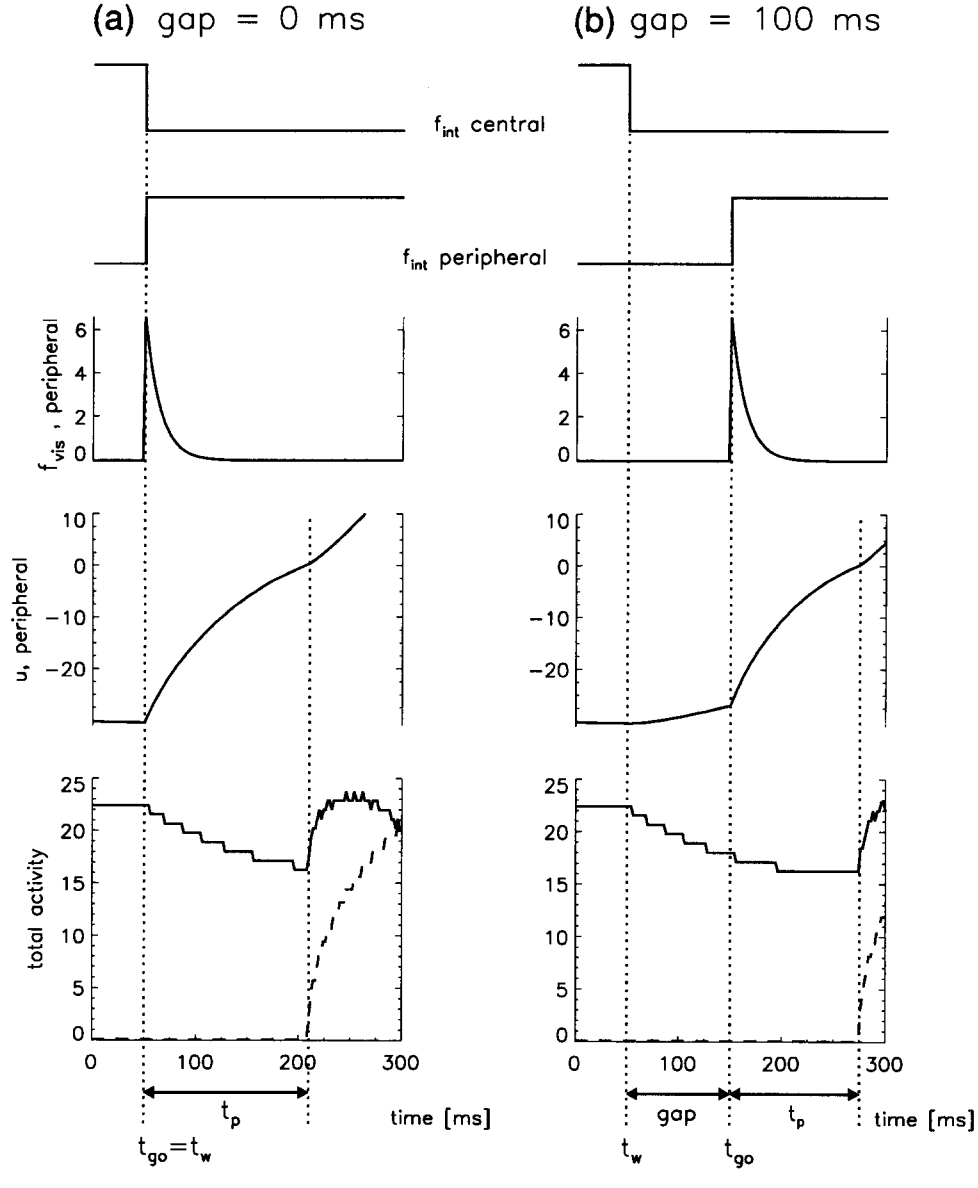

FIGURE 5. Time-course of relevant model quantities in the gap paradigm. Line types and notation as in Fig. 4. (a) Vanishing gap. (b) gap of 100 msec. From top to bottom: central intention (intention to fixate), peripheral intention, visual target information, field amplitude at target position, total activity (continuous line) and total, spatially weighted activity (dashed line). For details, see main text.

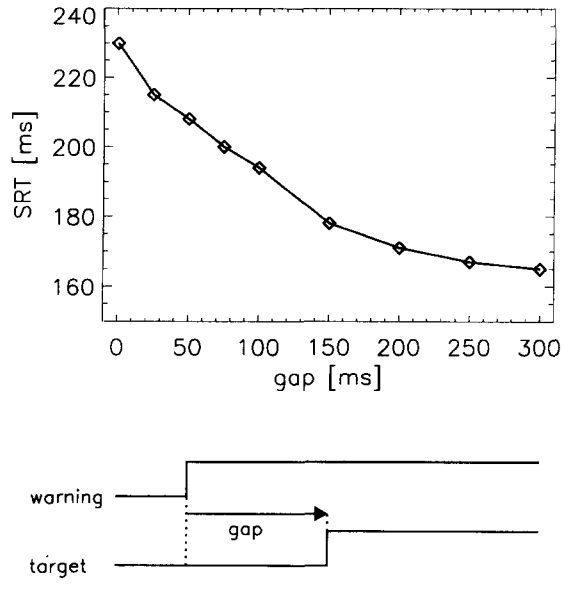

FIGURE 6. SRTs as a function of the gap interval. Here, a warning signal different from FP on- or offsets precedes target onset. From a maximum of 230 msec, SRT decays asymptotically to a level of 165 msec.

confirmed by Kingstone, Klein and Taylor (1995) using a peripheral visual warning (therein, see also their discussion of differences to acoustic warnings). The curve in Fig. 6 shows a steady decrease with increasing gap interval, reaching an asymptotic minimum for a gap of 300 msec. Studies of the gap effect show for some subjects a re-increase in SRTs when gap intervals are increased beyond 200–300 msec (e.g. Reulen, 1984a; Kalesnykas & Hallet, 1987), but, for instance, Ross and Ross (1980) increased the gap interval up to 600 msec using non-visual warnings without noticing any re-increase in SRTs. This finding is similar to the model results shown in Fig. 6, where a warning different from an FP on/offset was used. As shown in the next section, this behavior is different when an FP-offset acts as the warning.

As already depicted in Fig. 5, I distinguish between centrally located intention (intention to fixate) and a peripherally located intention. Accordingly, two amplitudes $k_{\text{int}}^{\text{cen}}$ and $k_{\text{int}}^{\text{per}}$ are introduced, measuring the strength of either intention. More generally, the amplitude k_{int} in equation (5) can be regarded as depending on the location x_0. In the model, this distinction is required due to the different functional roles of central and peripheral information.

As a reaction to the target appearance, visual as well as intentional information is taken to act concurrently onto a peripheral field region. The strengths of the individual contributions are adjusted such that peripheral intention evokes a movement even without visual information, but peripheral visual information alone is too weak to raise the field over threshold. This implies here the addressed nature of voluntary saccades as contrasted to purely stimulus driven, reflexive responses. However, the presence of FP offset and onset effects clearly supports the view that visual information is relevant for the timing of voluntary saccades as well. It would appear to be artificial to introduce a boundary which separates central and peripheral field regions by coupling visual information only to the central part. The consequences of this qualitatively equivalent treatment of central and peripheral visual information will be part of the Discussion.

3.3. Time-course of visual information: fixation on/offset effects

In the model, the primary role of visual information is to mediate the observed FP off- and onset effects. Within the dynamic field framework the integration of visual information is straightforward. Visual onsets are coupled with a positive sign to the field dynamics and visual offsets with a negative sign. In this way, central onsets contribute to a conservation of central activity on the field. Consequently, if centrally located intention is removed to allow for a movement into the periphery, it takes longer (compared to a missing FP onset) for the peripheral intention to raise the field above threshold because the central visual onset results in an additional inhibition at peripheral field locations. Similarly, due to the negative coupling, FP offsets weaken central activity, so that it becomes easier for peripheral intention to initiate a movement.

An additional assumption must be made with respect to the time-course of visual information in response to on- and offsets. These are regarded to act transiently onto the field dynamics and thus their action is of limited duration. This assumption is in line with experimental data, because it yields a realistic time-course of on/offset effects. To keep the number of parameters small, visual information is obtained by a low-pass filtering of on- and offset events, which is characterized by a transfer amplitude and a time constant. During simulation studies it turned out to be essential to distinguish explicitly between visual offsets and onsets in the sense, that for both, respectively, different time constants and transfer amplitudes must be introduced. This is required to adjust the amount of onset and offset effects independently from each other. In the model, the on/offset specificity of the temporal filter is dealt with by decomposing visual information into an on- and offset component and filtering each component separately:*

$$f_{\text{vis}}(t) = f_{\text{on}}(t) + f_{\text{off}}(t) \tag{8}$$

$$\tau_{\text{on}} \dot{f}_{\text{on}}(t) = -f_{\text{on}}(t) + R[\dot{s}(t)] \tag{9}$$

$$\tau_{\text{off}} \dot{f}_{\text{off}}(t) = -f_{\text{off}}(t) - R[-\dot{s}(t)] \tag{10}$$

$s(t)$ represents the visual stimulus, of which only the temporal change, $\dot{s}(t)$, is considered as relevant. Stimulus units are chosen such that onsets are represented by

*It is convenient to stay within the formalism of differential equations to describe all processes within the model by the same mathematical tools. The low-pass filtering may be as well described in terms of system theory, defining appropriate transfer functions. In the present case of linear dynamics, both descriptions can be easily transformed into each other.

a unit step-function. $R(\cdot)$ is a ramp function (with $R(y)=y$ for $y>0$ and $R(y)=0$ otherwise) which is used to distinguish between on- and offsets. The time-course of visual information is shown in Fig. 7. The choice of transfer amplitudes and time constants is discussed now.

Extending the parameterization of the spatial shape of visual information (*cf.* equation 5), two transfer amplitudes k_{on} and k_{off} are introduced. Similarly to the treatment of intentional information, I distinguish between transfer amplitudes of central and peripheral visual information, respectively. The central amplitudes, k_{off}^{cen} and k_{on}^{cen}, are set to gain a reasonable on/offset effect for a vanishing gap. When compared to complete overlaps, this effect is adjusted to be approximately 30 msec for offsets and 15 msec for onsets (Ross & Ross, 1981). The visual time constants τ_{on} and τ_{off} affect the detailed shape of gap/overlap curves. τ_{off} is set to find a significant offset effect also for gaps as large as 200 msec. The onset time constant is adjusted on the basis of the observation that SRTs show a steady increase if the FP onset follows the target, taking on a maximum for overlaps of ≈ 100 msec (Ross & Ross, 1981). If onset information decays too slowly, no further prolongation of SRTs is observed if the overlap interval is increased above zero. This is the main reason for introducing separate filters for on- and offsets, respectively. In particular, onsets decay faster than offsets and a higher transfer amplitude, k_{on}^{cen}, is attributed to them (*cf.* Fig. 7 and Table A1).

The gap/overlap curves where FP on/offsets act as a warning signal are shown in Fig. 8. For positive gaps, the on/offset events are taken to act also as a warning, for negative gaps the target onset acts as the warning. Figure 8 shows that the model successfully integrates the action of warnings, FP onset and FP offsets. Although parameters are adjusted on the basis of only two observations for each curve (effect of FP on/offset for vanishing gap, amount of offset effect for large gaps and amount of onset effect for 100 msec overlap) the model generalizes well to other gap values in agreement with,

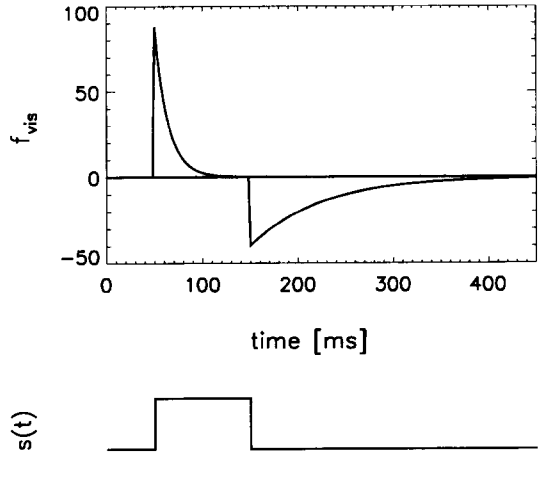

FIGURE 7. Time-course of visual information, f_{vis}, at the central position in response to a foveal stimulus, $s(t)$. Responses to on- and offsets differ by amplitude and time constant.

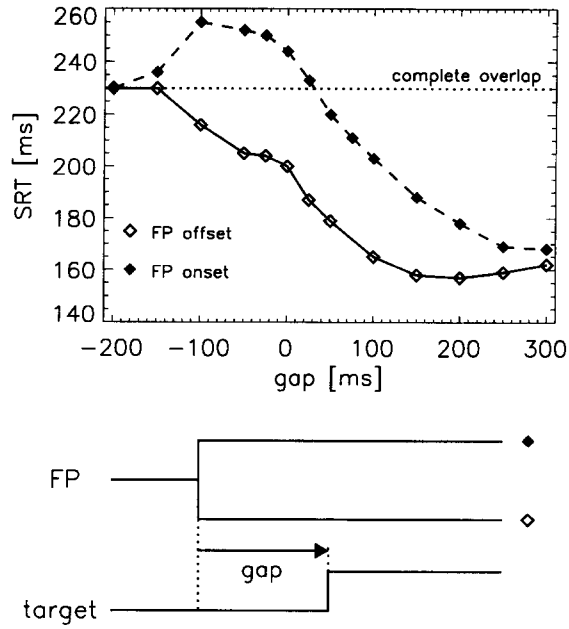

FIGURE 8. SRT as a function of the gap interval in FP offset (open symbols) and FP onset (solid symbols) conditions. For negative gaps (overlaps) both curves converges to the level indicated by "complete overlap" characterized by no change in the FP. For large positive gaps, the visual transients do not affect SRTs any more, so that both curves converge to the level related to the pure preparation effect. The two FP traces in the depicted stimulus protocol are related to FP on- and offset, respectively, as indicated by the symbols close to the traces.

e.g. Ross and Ross (1980, 1981). For large overlaps both curves approach the level of complete overlap, where changes in the FP occur too late to affect reaction times. Due to the transient action of visual information the effects of on/offsets are restricted to certain gap intervals. Thus, both curves reach the asymptotic value of 165 msec for gaps larger than 300 msec. This level is given by the asymptotic size of the general preparation effect (*cf.* Fig. 6). The offset curve shows a minimum at a gap of 200 msec, before reaching the asymptotic level. The FP offset reduces SRTs as compared to the pure preparation effect (*cf.* Fig. 6), but the offset curve must also converge to the preparation asymptote, so that an increase in SRTs occurs at intermediate gap intervals. The exact position of this minimum is given by the time constant of the visual offset transient. The opposite reasoning holds for the onset curve. Onsets prolongs latencies as compared to non-visual warnings, but, for large overlaps, the same asymptote must be approached as for non-visual warnings. Consequently, the onset curve shows a relative maximum, the position of which is determined by the time constant of the onset transient.

As discussed in the previous section, several non-compatible reports about a re-increase of SRTs for large gap intervals can be found in the literature. Results from my model suggest that at least one component of an observed re-increase might be due to the transient nature of visual information. This is compatible with the data of Ross and Ross (1981, their Fig. 1) who observed no re-increase for auditory warnings, but a minimum for FP offsets warnings. These comparisons remain

episodic, and more systematic experimental studies are needed to test for a relation between visual transients and re-increases in reaction time.

4. DISCUSSION

A functional model of the part of the saccadic system relevant for movement initiation was proposed. Specifically, I addressed behavioral data from gap/overlap paradigms in which strong effects in SRTs can be induced. The theoretical framework is based mainly on three principles: (1) The state of the saccadic system relevant to movement initiation can be described by a certain readiness. The time-course of readiness in conjunction with a threshold criterion determines SRTs. (2) Effects of visual and intentional information on SRTs are dealt with by defining readiness dynamics to which these kinds of information are coupled. (3) The spatial generalization of readiness dynamics (field dynamics) raises the problem of possibly incompatible intentional and visual movement goals. This can be solved by defining inhibitory interactions within the field.

These three principles led in a rather natural way to the framework of neural, dynamic fields. It was shown that within this framework it is possible to integrate several experimental findings resulting from the isolated and combined action of different components contributing to gap/overlap curves. The consistent reproduction of experimental results was based on a particular conception of *motor preparation*. Movements are prepared for by removing the intention to fixate. This does not imply having an intention to move somewhere. It is the temporal dissociation between motor preparation and intention to move which, in my view, reflects the situation prepared by the gap paradigm. Further, within the spatially continuous scheme, intentions to move and not to move (i.e. to fixate) are not categorically different. The latter is only distinguished by its action onto the central field.

Before discussing more relations to experimental data, I want to comment on the conceptual standing of the theoretical framework of dynamic fields. Due to the presence of a representation of visual, or movement space, there is no intrinsic separation between the decision *where* to go and *when* to go. I view this as a prerequisite for models addressing interactions between saccade metrics and saccadic reaction times, like revealed, e.g. in double-step paradigms (one target stepping twice). Kopecz and Schöner (1995) showed that target selection within the saccadic system can be understood within a similar theoretical framework. Thus, a coherent understanding of metrical and reaction time aspects might be provided by this setting. Other quantitative, theoretical works on reaction times mostly address statistical aspects of reaction time distributions (see Pacut, 1977 for an overview), whereas here the relation to the behavioral context is emphasized, as well as the integration aspect. The yet most quantitative model of SRTs in gap/overlap paradigms was proposed by Reulen (1984a, b). Aside from the theoretical framework, an important conceptual difference between Reulen's and this model is the significance attributed to intentional information here. Reulen did not distinguish between the general preparation effect and on/offset effects, so that he implicitly referred to the visual effects, which he mapped on a facilitation of sensory processing. This relation between offset effect and enhanced sensory processing was later rejected experimentally by Reuter-Lorenz *et al.* (1991), by carefully distinguishing between offset effect and warning effect.

The used here summation of visual and intentional information (*cf.* equation 4) to act jointly on one decision stage yields a simple prediction: SRTs of visually guided saccades should be shorter than SRTs to targets which are only defined by intention. If intentional and visual information both act on the readiness dynamics, they raise the peripheral field faster over threshold as compared to the case of having only intentional information available. A reduced SRT of visually guided saccades compared to memory guided saccades has been reported, e.g. by Smit, van Gisbergen and Cools (1987), which indeed can be interpreted in the sense of summation.*

Other types of information can be treated in the same way, for instance, pre-information based on prior knowledge about target locations. The action of pre-information could be to pre-shape the field at expected locations and thus bring it closer to threshold. This, in turn, would decrease SRTs to targets in expected locations as indeed observed by Kowler *et al.* (1984). This integration aspect of dynamic fields is in line with recent contributions to the question whether reaction times are the outcome of a so-called race architecture (independent decision stages attributed to different sensory modalities), or whether they show the behavior expected from a summation structure (convergence of different types of sensory information at a decision stage). The results of Hughes, Reuter-Lorenz, Nozawa and Fendrich (1994), who studied the statistics of reaction times of responses to redundant target information, support the view of central summation stages where sensory information converges. My model is clearly of this summation type and it extends the summation concept from purely sensory signals to internally generated signals like intention, or expectation.

4.1. *Predictions of the model*

To check further the validity of principles underlying the model, simulations of two experimental protocols are done, which go beyond the usual gap/overlap paradigms. The first mimics an experiment done by Braun and Breitmeyer (1990), who performed a gap paradigm using the FP offset as a warning, 200 msec before target onset. Further, they let the FP reappear after a variable period (the off interval), measured from FP offset. The outcome of the corresponding simulations is shown in

*It would not be "fair" to refer to anti-saccades to support the prediction, because in that case, some time-consuming spatial transformation is needed to find the saccadic goal (see below).

Fig. 9 together with the experimental protocol. Consistent with Braun and Breitmeyer one observes a dependency on the off interval showing a maximal SRT at time of target onset. The variations in SRT induced by this paradigm are about 25 msec in the simulation (excluding the condition of vanishing off interval equivalent to a complete overlap, for which no data point is plotted in Fig. 9), whereas Braun and Breitmeyer found variations of more than 50 msec. But, importantly, these authors also included express saccades in their mean SRTs, which were strongly suppressed when the FP reappeared around the time of target onset. Thus, the effect on regular saccades (which they did not report separately) can be expected to be smaller.

The second simulated experimental protocol, to my knowledge, has never been reported in the literature. The outcome of these simulations is intimately linked to the assumption on the stationary state of field dynamics (*cf.* Section 3.1). There, the parameter regime was used, where an activated region persists even without external inputs, i.e. without visual and intentional information. The alternative was to have an equilibrium without any activity, i.e. a subthreshold equilibrium. But how can, operationally, the case of self-generated activity be distinguished from having field dynamics with a subthreshold equilibrium? Also in the latter case a certain reaction time would be observed, because the field is subthreshold everywhere, in particular, in the periphery. But there is a crucial question, the answer to which can rule out one of the two cases: if the system is prepared to be in a state of "optimal readiness" by a preceding warning event, does the offset of the FP at the time of target onset reduce the reaction time further? This situation of "optimal readiness" can be prepared using a warning signal leading to a decay of the central field to its resting level before a target appears. If there is a certain amount of persistent activity, an FP offset applied simultaneously with the target stimulus, will reduce this central activity further, which in turn decreases peripheral inhibition, resulting in a reduced SRT when compared to no FP offset. If the state of "optimal readiness" corresponds to a subthreshold field distribution, the FP offset will inhibit the central field further, but without any effect on peripheral field locations, because the lateral interaction within the field is mediated only by activity, requiring a suprathreshold field (*cf.* Section 3.1). Thus, no difference between applying an FP offset or not applying it will be observed. This illustrates that an experimental test can be designed to distinguish between these two alternatives.

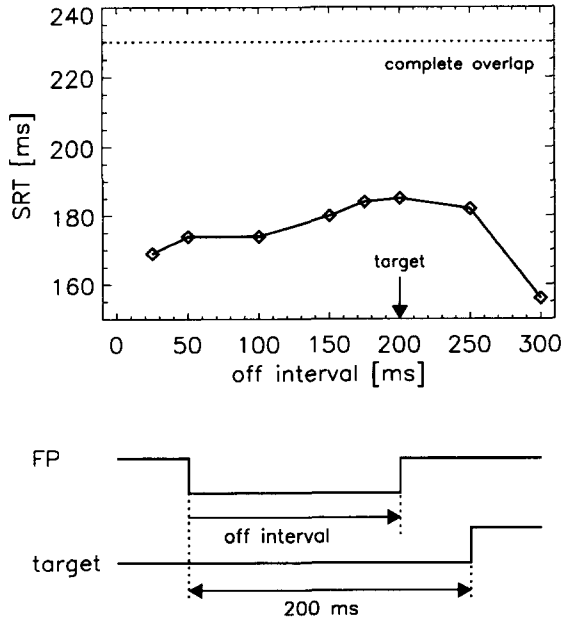

FIGURE 9. SRTs in a simulated Braun and Breitmeyer paradigm (1990). The fixation point reappears after a variable interval. The time of target onset is indicated by the arrow labeled "target". The time between FP offset and target onset is held constant (200 msec). The SRT is maximal when the FP is turned on simultaneously with target onset.

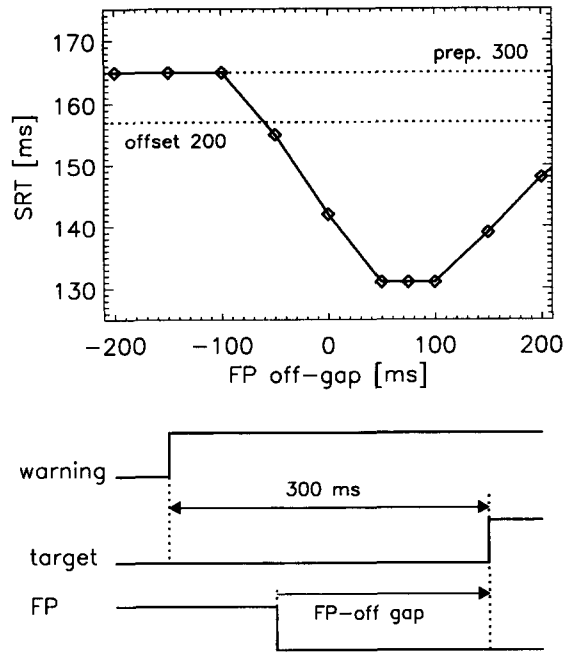

FIGURE 10. Effect of a temporal dissociation of warning and FP offset on SRTs. The line labeled "prep. 300" indicates the minimal SRT induced by the preparation effect (*cf.* Fig. 6). The line labeled "offset 200" indicates the SRT found in the simulations of the FP offset paradigm with a gap of 200 msec. This is the minimal SRT found in simulations of "traditional" gap paradigms shown before. Importantly, in the model, SRTs can be reduced further by a temporal dissociation of warning and FP offset.

To study the behavior in the case of self-generated activity, we simulated a paradigm where a warning is given (300 msec before target onset), followed by an FP offset after a variable period (*cf.* Fig. 10). SRTs as a function of the gap between FP offset and target onset (FP-off gap) are shown in Fig. 10. For negative FP-off gaps (offset after target onset), SRTs converge to the value found for the pure preparation effect at a gap of 300 msec (*cf.* Fig. 6), because the offset is too late to interfere with the creation of peripheral activity. More important, most of the SRTs are below the level given by the minimal SRT observed in conditions where the

FP offset acts simultaneously as a warning. This is indicated by the line labeled "offset 200" (*cf.* Fig. 8). Further, a characteristic minimum can be observed at an FP-off gap of 75 msec. Thus, a prediction is that when dissociating warning and FP offset in time, SRTs can be decreased below the level observed in "traditional" gap conditions, where the offset is also used as a warning. As discussed above, this prediction is linked to the assumption on the nature of the stationary states of autonomous field dynamics.

One reason for distinguishing between general warnings and FP offsets as independent factors contributing to the gap effect is the "response specificity" of FP offsets. Ross and Ross (1981) demonstrated that FP offsets reduce manual reaction times no more than acoustic warnings do. This was found to be in contrast to ocular responses. Reuter-Lorenz *et al.* (1991) restricted this specificity further to visually guided saccades based on their finding that FP offsets, applied independently from a warning, did not reduce reaction times in the anti-saccade task. This was questioned by Fischer and Weber (1993, p. 598) who reported on reduced SRT due to FP offsets in the anti-saccade task, even if the warning was controlled. My model includes a simple mechanism which might be responsible for "response specificities" as such, as well as for the conflicting results in the literature. The key feature is the transient nature of visual information, which lets an FP offset interfere only for a limited period of time with the decision to initiate the movement. In the simulated gap experiments presented so far, one can observe this interference for most of the gap intervals used, because the target appearance immediately (after the afferent delay) triggered a corresponding intention to move. This appears to be a reasonable assumption, because no further transformation of the retinal error into a displacement is required. Both quantities are identical due to the experimental setup. The situation changes in the anti-saccade task. Here, the required displacement must be first derived from the retinal error. In view of the observed increasing SRTs (Hallet, 1978), it is obvious that this process requires some time. Interpreting this finding in terms of the scheme in Fig. 1, the action of visual information and the action of the intention to move to a non-visually defined location become separated in time due to the required spatial transformation, which is thought to take place at the level labeled "instruction". If this additional "transformation time" is large enough, one can expect that visual information has decayed completely due to its transient nature, so that no interference with intentional information is observed any more.

To demonstrate this effect, results from a simulated paradigm of Reuter-Lorenz *et al.* (1991) are shown in Fig. 11. A warning signal is given 200 msec before target onset simultaneously with the FP offset (FP-gap condition). The SRTs obtained are compared to the condition where only the warning had been given, without changes in the FP (FP-overlap condition). To simulate the effect of response mode (visually-guided, or "anti"), a delay, t_T, is introduced between the time visual target information is received and the onset of the intention to move. This mimics the additional transformation time required in the anti-saccade task. In Fig. 11, FP-gap and FP-overlap conditions are compared. One clearly observes that the benefit from the FP offset decreases with increasing t_T and thus with increasing reaction time. In this sense, the model effect of FP offsets is not specific for responses, but simply a function of the total reaction time. This might explain findings reported by Fischer and Weber (1993, p. 598). In their study of anti-saccades (Fischer & Weber, 1992, 1993) they found mean anti-SRTs (in FP-gap conditions) of approximately 180 msec and found a benefit from FP offsets, whereas Reuter-Lorenz *et al.* (1991) reported mean anti-SRTs in the same condition of more than 220 msec and found no significant benefit from FP offsets.

The model results suggest that the reaction time as such may be at least one component contributing to the amount of FP offset effects, but it might also be important in which way the SRT is manipulated. For instance, Reuter-Lorenz *et al.* (1991) found no change in the benefit from FP offsets, if SRTs are increased by using dim targets. However, the appropriate way to test for FP interferences should be to locate the FP offset (or onset) at a point in time which is close to the reaction time of the response mode under study. In this way, one could also reconsider the question whether manual responses are affected by FP changes. For instance, Ross and Ross (1981) found manual reaction times of about 460 msec in conditions of complete overlap but they extended their overlap interval only up to 300 msec. To test for FP interferences, an overlap of 450 msec would have been more appropriate.

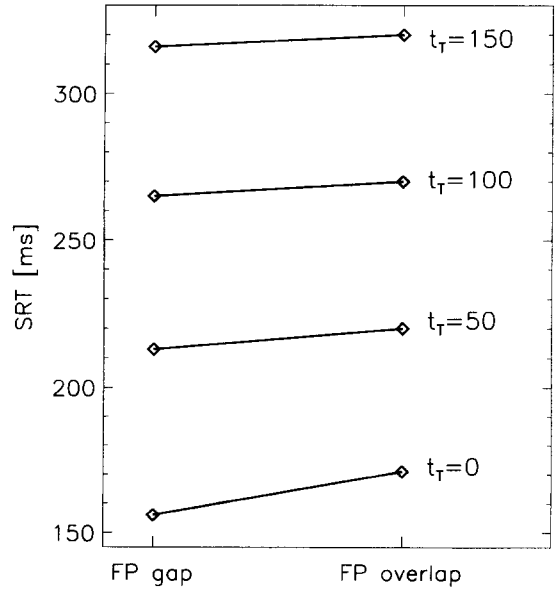

FIGURE 11. Comparison between SRTs from FP gap (FP offset 200 msec before target onset) and FP overlap conditions (no change of FP) for different "transformation times", t_T. In every condition a warning signal precedes target onset by 200 msec. The benefit from FP offset decreases with increasing t_T from 15 to 4 msec.

4.2. Limits and extensions of the model

Although I distinguished between central and peripheral information, by construction, dynamic fields are predestined to deal with visual space not only categorically, but to treat it as a continuum from center to periphery. In the simulations shown so far, target locations are chosen such that peripheral information has no spatial overlap with central activity. As far as this condition is fulfilled, reaction times do not depend on target distance. Activity dynamics change qualitatively if this spatial overlap occurs (in the model at eccentricities smaller than 25°). Then, an activated region does not grow at its final peripheral position at the cost of central activity, but central activity is drawn continuously to the location specified by the external input. Consequently, the total, spatially weighted activity shows a slow increase from the time the go signal is received. This behavior is not consistent with my previous definition of the reaction time, because now, the weighted total activity increases immediately from zero, which would correspond to a vanishing internal processing time. But the threshold criterion was chosen rather arbitrarily. Using a higher threshold, one observes that the processing time increases with decreasing target amplitude and even diverges. Clearly, such a strong increase has not been observed experimentally for all amplitudes smaller than 25°. But, importantly, the trivial *linear mapping* of visual space onto the field coordinate, x, was used and the width of active regions on the field as well as the widths of input information were not varied systematically. To relate better to experimental data it would be adequate to use a *logarithmic mapping* of visual space which is found, e.g in the Superior Colliculus of monkeys (Ottes, van Gisbergen & Eggermont, 1986). Then, the increase in SRT can be expected to occur at much smaller amplitudes which may be consistent with the observed strong increase in SRTs at amplitudes below 1° (Weber, Aiple, Fischer & Latanov, 1992), or below 0.5° (Wyman & Steinman, 1973). Thus, to relate the model to this spatial aspect of SRTs, mapping functions must be introduced and relevant widths must be varied.

Although the gap paradigm often induces express saccades, this type of response can be viewed as a reflexive response mode, different from intended movements (*cf.* Introduction). Thus, to construct a model of SRTs not including express saccades is a reasonable approach. The difference between regular and express responses with respect to their dependence on behavioral relevant information (e.g. express saccades can only be made to targets defined by an onset) suggests that a different processing stage is involved in the generation of express saccades with its own relation to visual and intentional information. Nevertheless, this processing stage must be somehow coupled to the level relevant for the initiation of regular saccades. An extension of the model presented here which includes express saccades is currently under investigation.

4.3. Relation to neurophysiology

Although derived from functional requirements, some working principles of the model can be compared to the organization and behavior of neural structures. The topographic representation of visual or movement space is a well known property of neural systems. In particular, the Superior Colliculus is probably the best studied structure with respect to the way space and movements are represented in mammals and which has intimate relations to saccadic eye movements (see e.g. Sparks, 1988 for a review). I will restrict my discussion mainly to collicular behavior, but many similar features had been described also in cortical areas. The behavior of collicular neurons is, of course, much more complex than the phenomenology shown by our model, but some common features are obvious. (1) Sensory space is coded in a retinotopic map and movements are coded by relative displacements. (2) A large portion of neural tissue is active before a movement. Movements are represented by a population code (Lee, Rohrer & Sparks, 1988; van Gisbergen, van Opstal & Tax, 1987). (3) Evidence for lateral inhibitory interactions has been accumulated (e.g. by Douglas & Anderchek, 1991).

In the model, a consequence of its retinotopic organization is the existence of "cells" related to fixations. Comparable cells had been studied in the Colliculus of cat and monkey (Peck, 1989; Munoz & Guitton, 1991; Munoz, Guitton & Pélisson, 1991; Munoz & Wurtz, 1993). Cells in the rostral pole of the Superior Colliculus, where the central visual field is represented, and movement related cells were found to show an approximately reciprocal pattern of activity. Fixation cells are active during periods of active fixation (even without a physical fixation target), whereas they pause during saccades. Movement cells show a reciprocal behavior, pointing at a mutually inhibitory interaction (Munoz & Wurtz, 1993). In my model, activity at the central field region can be well compared to real fixation cell excitation. First, the reduction of central activity is a prerequisite for movement initiation, and second, central activity does not depend solely on visual input. When identifying "fixation cells" in the model with real fixation cells, the prediction arises that they reduce their population activity during a gap period. Munoz and Wurtz (1993) studied the activity of fixation cells during a blink of the fixation point, but importantly, their monkeys were instructed to keep the eyes stationary. Thus, no sign of "motor preparation" in the sense of removing the intention to fixate can be expected. To test this prediction, the gap paradigm has to be done while recording from fixation cells.

More indirect evidence for an identification of the model with fixation cell behavior is given by the breakdown of the hypothesis of mutual inhibition between fixation cells and movement related cells in its absolute form. Activity of both cell types is reciprocally related only for large saccades. Munoz and Wurtz (1993) found cells classified as "fixation" which did not pause for saccades up to 15° amplitude and even showed a

movement related burst of activity. In this sense, a cell can be both of the fixation and the movement type. The proposed dichotomy must be seen as an approximation which is valid for large saccades only. This continuum between movement and fixation is a natural property of the field framework, because large portions of the field are activated simultaneously. It occurs in the spatial overlap situation discussed above, in which a point on the field is part of the centrally located activity and peripheral activity, simultaneously.

Other types of pre-saccadic activity can be observed in neural structures (e.g. Schall & Hanes, 1993; Glimscher & Sparks, 1992), but a comparison with model features would be too speculative due to the very simple (all-or-nothing) activity measures used in the model.

4.4. Conclusion

In this study it was shown that within the framework of dynamic fields, the effects of the timing of general warnings and FP off- and onset on the reaction time of saccadic eye movements can be successfully modeled. The simulated data shown in Figs 8, 9 and 10 reproduces well-known experimental results and includes testable predictions. The outcome of these different experimental protocols can be understood by the concept of integrating intentional and visual information by their joint action on readiness dynamics. Although the theoretical setting is derived from a functional reasoning based on behavioral data, similarities to neural design and working principles are observed. This shows how a functional analysis of behavior can lead to questions relevant to neurophysiology.

REFERENCES

Amari, S. (1977). Dynamics of pattern formation in lateral-inhibition type neural fields. *Biological Cybernetics, 27*, 77–87.

Amari, S. (1989). Dynamical stability of formation of cortical maps. In Arbib, M. A. & Amari, S. (Eds), *Dynamic interaction in neural networks: models and data* (pp. 15–34). Berlin, Springer.

Amari, S. & Arbib, M. A. (1977). Competition and cooperation in neural nets. In Metzler, J. (Ed.), *Systems neuroscience* (pp. 119–165). London, Academic Press.

Becker, W. & Jürgens, R. (1979). An analysis of the saccadic system by means of double step stimuli. *Vision Research, 19*, 967–983.

Boch, R. & Fischer, B. (1986). Further observations on the occurrence of express-saccades in the monkey. *Experimental Brain Research, 63*, 487–494.

Braun, D. & Breitmeyer, B. G. (1990). Effects of reappearance of fixated and attended stimuli upon saccadic reaction time. *Experimental Brain Research, 81*, 318–324.

Chipalkatti, R. & Arbib, M. A. (1987). The prey localization model: a stability analysis. *Biological Cybernetics, 57*, 287–299.

Chipalkatti, R. & Arbib, M. A. (1988). The cue interaction model of depth perception: a stability analysis. *Journal of Mathematical Biology, 26*, 235–262.

Douglas, R. M. & Anderchek, K. E. (1991). Identification of cells in the superior colliculus subject to widespread inhibition. In *Society of Neuroscience Abstracts* (Vol. 12, p. 1379).

Fischer, B. & Boch, R. (1983). Saccadic eye movements after extremely short reaction times in the monkey. *Brain Research, 260*, 21–26.

Fischer, B. & Ramsperger, E. (1984). Human express saccades: extremely short reaction times of goal directed eye movements. *Experimental Brain Research, 57*, 191–195.

Fischer, B. & Weber, H. (1992). Characteristics of "anti" saccades in man. *Experimental Brain Research, 89*, 415–424.

Fischer, B. & Weber, H. (1993). Express saccades and visual attention. *Behavioral Brain Sciences, 16*, 553–610.

van Gisbergen, J. A. M., van Opstal, A. J. & Tax, A. A. M. (1987). Collicular ensemble coding of saccades based on vector summation. *Neuroscience, 21*, 541–555.

Glimscher, P. W. & Sparks, D. L. (1992). Movement selection in advance of action in the superior colliculus. *Nature, 355*, 542–545.

Hallet, P. E. (1978). Primary and secondary saccades to goals defined by instructions. *Vision Research, 18*, 1279–1296.

Heywood, S. & Churcher, J. (1980). Structure of the visual array and saccadic latency: implications for oculomotor control. *Quarterly Journal of Experimental Psychology, 32*, 335–341.

House, D. H. (1988). A model of the visual localization of prey by frog and toad. *Biological Cybernetics, 58*, 173–192.

Hughes, H. C., Reuter-Lorenz, P. A., Nozawa, G. & Fendrich, R. (1994). Visual-auditory interactions in sensorimotor processing: saccades versus manual responses. *Journal of Experimental Psychology and Human Perception Performance, 20*, 131–153.

Kalesnykas, R. P. & Hallet, P. E. (1987). The differentiation of visually guided and anticipatory saccades in gap and overlap paradigms. *Experimental Brain Research, 68*, 115–121.

Kingstone, A. & Klein, M. (1993a). Visual offsets facilitate saccadic latency: does preangagement of visuospatial attention mediate this gap effect. *Journal of Experimental Psychology and Human Perception Performance, 19*, 1251–1265.

Kingstone, A. & Klein, M. (1993b). What are human express saccades? *Perception Psychophysics, 54*, 260–273.

Kingstone, A., Klein, R. M. & Taylor, T. (1995). Visual offsets facilitate saccadic latency: there are two components to this gap effect. *submitted.*

Kopecz, K. & Schöner, G. (1995). Saccadic motor planning by integrating visual information and expectation on neural dynamic fields. *Biological Cybernetics*, in press..

Kowler, E., Martins, A. J. & Pavel, M. (1984). The effect of expectations on slow oculomotor control—IV. Anticipatory smooth eye movements depend on prior target motions. *Vision Research, 24*, 197–210.

Lee, C., Rohrer, W. H. & Sparks, D. L. (1988). Population coding of saccadic eye movements by neurons in the superior colliculus. *Nature, 332*, 357–360.

McPeek, R. M. & Schiller, P. H. (19940. The effects of visual scene composition on the latency of saccadic eye movements of the rhesus monkey. *Vision Research, 34*, 2293–2305.

Munoz, D. P. & Guitton, D. (1991). Control of orienting gaze shifts by the tectoreticulospinal system in the head-free cat. II. Sustained discharges during motor preparation and fixation. *Journal of Neurophysiology, 66*, 1624–1641.

Munoz, D. P. & Wurtz, R. H. (1993). Fixation cells in monkey superior colliculus. I. Characteristics of cell discharge. *Journal of Neurophysiology, 70*, 559–575.

Munoz, D. P., Guitton, D. & Pélisson, D. (1991). Control of orienting gaze shifts by the tectoreticulospinal system in the head-free cat. III. Spatiotemporal characteristics of phasic motor discharges. *Journal of Neurophysiology, 66*, 1642–1666.

Nothdurft, H. C. & Parlitz, D. (1993). Absence of express saccades to texture or motion defined targets. *Vision Research, 33*, 1367–1383.

Ottes, F. P., van Gisbergen, J. A. M. & Eggermont, J. J. (1984). Metrics of saccade responses to visual double stimuli: two different modes. *Vision Research, 24*, 1169–1179.

Ottes, F. P., van Gisbergen, J. A. M. & Eggermont, J. J. (1986). Visuomotor fields of the superior colliculus: a quantitative model. *Vision Research, 26*, 857–873.

Pacut, A. (1977). Some properties of threshold models of reaction latency. *Biological Cybernetics, 28*, 63–72.

Peck, C. K. (1989). Visual responses of neurons in cat superior colliculus in relation to fixation of targets. *Journal of Physiology, 414*, 301–315.

Reulen, J. P. H. (1984a). Latency of visually evoked saccadic eye

movement. I. Saccadic latency and the facilitation model. *Biological Cybernetics, 50*, 251–262.

Reulen, J. P. H. (1984b). Latency of visually evoked saccadic eye movements. II. Temporal properties of the facilitation mechanism. *Biological Cybernetics, 50*, 263–271.

Reuter-Lorenz, P. A., Hughes, H. C. & Fendrich, R. (1991). The reduction of saccadic latency by prior offset of the fixation point: an analysis of the gap effect. *Perception Psychophysics, 49*, 167–175.

Rohrer, W. H. & Sparks, D. L. (1993). Express saccades: the effect of spatial and temporal uncertainty. *Vision Research, 33*, 2447–2460.

Ross, L. E. & Ross, S. M. (1980). Saccade latency and warning signals: stimulus onset, offset, and change as warning events. *Perception Psychophysics, 27*, 251–257.

Ross, S. M. & Ross, L. E. (1981). Saccade latency and warning signals: effects of auditory and visual stimulus onset and offset. *Perception Psychophysics, 29*, 429–437.

Saslow, M. G. (1967). Effects of components of displacement-step stimuli upon latency of saccadic eye movements. *Journal of the Optical Society of America, 57*, 1024–1029.

Schall, J. D. & Hanes, D. P. (1993). Neural basis of saccadic target selection in frontal eye field during visual search. *Nature, 36*, 467–469.

Smit, A. C. & van Gisbergen, J. A. M. (1989). A short latency in saccade dynamics during square-wave tracking and its significance for the differentiation of visually guided and predictive saccades. *Experimental Brain Research, 76*, 64–74.

Smit, A. C., van Gisbergen, J. A. M. & Cools, A. R. (1987). A parametric analysis of human saccades in different experimental paradigms. *Vision Research, 27*, 1745–1762.

Sommer, M. A. (1994). Express saccades elicited during visual scan in the monkey. *Vision Research, 34*, 2023–2038.

Sparks, D. L. (1988). Neural cartography: sensory and motor maps in the superior colliculus. *Brain Behavior Evolution, 31*, 49–56.

Weber, H., Aiple, F., Fischer, B. & Latanov, A. (1992). Dead zone for express saccades. *Experimental Brain Research, 89*, 214–222.

Wenban-Smith, M. G. & Findlay, J. M. (1991). Express saccades: is there a separate population in humans? *Experimental Brain Research, 87*, 218–222.

Wheeless, L. L., Cohen, G. H. & Boynton, R. M. (1967). Luminance as a parameter of the eye-movement control system. *Journal of the Optical Society of America, 57*, 394–400.

Wyman, D. & Steinman, R. M. (1973). Latency characteristics of small saccades. *Vision Research, 13*, 2173–2175.

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APPENDIX

Let $\bar{d}$ be the stationary width of an activated region on the field without external inputs. Then, as derived by Amari (1977), $\bar{d}$ must be a zero of the function

$$g(d) = W(d) - u_0, \quad \text{with:} \quad W(d) = \int_0^d w(x)\,dx \qquad \text{(A1)}$$

with the interaction kernel $w(x)$ given by equation (6). Zeros of negative and positive slope belong to stable and unstable clusters of activity, respectively. Using a $w(x)$ with local excitation and long-range inhibition results in having either no zero, two zeros (with a positive and negative slope, respectively), or one zero with a negative slope (see also Kopecz & Schöner, 1994). The latter happens for $u_0 < 0$. In this case the only stationary solution is a stable cluster of activity. In the model, this parameter regime is regarded as relevant.

To simplify the discussion of parameter settings, it is helpful to distinguish between parameters which are "critical" with respect to the studied gap effect and others the value of which can be set almost arbitrarily. These "uncritical" parameters are mostly related to the spatial width of activity clusters (u_0, H, k_u, σ_u in equations 4 and 6, and the width of visual and intentional information (σ_{vis} and σ_{int} in equation 5). In simulations shown here, uncritical parameters are chosen such that no spatial overlap between central activity and peripheral, external information occurs. The case of spatial overlap is considered in the Discussion. A further uncritical parameter is the time constant τ_u in equation (4), in the sense that it only affects the overall time scale, but not relative relations among SRTs across different stimulus conditions. Critical to the time-course of the different components of the gap effect are amplitudes of external information (k_{on}^{cen}, k_{off}^{cen}, k_{on}^{per}, k_{int}^{cen}, k_{int}^{per}) and the time constants of visual information, τ_{on} and τ_{off}. Because the amount of central intention (intention to fixate) determines the initial amount of activity when a warning is perceived, k_{int}^{cen} determines the gap interval at which no more benefit is seen when increasing the gap further. The duration of decay of central activity during a gap interval increases with increasing initial activity. Thus, k_{int}^{cen} determines the time-course and amount of the preparation effect (*cf.* Fig. 6). The absolute SRTs observed are mainly determined by the strength of peripheral intention (intention to move somewhere). The larger k_{int}^{per} the faster the peripheral field is raised above threshold. The amplitude of peripheral visual information, k_{on}^{per}, contributes to SRTs as well, but this contribution is small due to $k_{int}^{per} > k_{on}^{per}$ with a ratio of 4.2 (*cf.* Section 3.2 and Table A1). The role of the visual time constants and amplitudes is discussed in Section 3.3.

TABLE A1. Model parameters used in simulations

Field dynamics	Visual information	Intentional information
$\tau_u = 0.75$ sec	$\tau_{on} = 0.015$ sec	$\sigma_{int} = 8$ deg
$\sigma_u = 6$ deg	$\tau_{off} = 0.075$ sec	$k_{int}^{per} = 27.7$
$k_u = 2.8$	$\sigma_{vis} = 6$ deg	$k_{int}^{cen} = 26.4$
$H = 1.5$	$k_{on}^{per} = 6.6$	
$u_0 = -3$	$k_{on}^{cen} = 88.0$	
$R = [-20°, 60°]$	$k_{off}^{cen} = 26.4$	

A list of the parameter values used for all simulations shown is given in Table A1. The differential equation (4) was integrated in time using a simple Euler method with a time step of $dt = 2 \cdot 10^{-3}$ sec. Space was discretized using a grid of 311 points from which the central 181 space points were taken to span the retinal interval $R = [-20°, 60°]$. The remaining "frame" of grid points was used to avoid border effects. With these settings the retinal discretization is 0.44°. The Gaussian part of the interaction kernel (6) was sampled over a range of $7\sigma_u$. For visual and intentional information a range of $5\sigma_{vis}$ and $5\sigma_{int}$ was used, respectively.